Topic 3 - ...
Case 1

M. B 166 (2)

ORONO

BULLETIN No. 166. **MARCH, 1909.**

INHERITANCE OF FECUNDITY.

CONTENTS.

MAINE
AGRICULTURAL EXPERIMENT STATION
ORONO, MAINE.

THE STATION COUNCIL.

PRESIDENT GEORGE E. FELLOWS	*President*
DIRECTOR CHARLES D. WOODS	*Secretary*
JOHN A. ROBERTS, Norway	*Committee of Board of Trustees*
CHARLES L. JONES, Corinna	
SAMUEL W. GOULD, Skowhegan	
AUGUSTUS W. GILMAN, Foxcroft	*Commissioner of Agriculture*
EUGENE H. LIBBY, Auburn	*State Grange*
CHARLES S. POPE, Manchester	*State Pomological Society*
RUTILLUS ALDEN, Winthrop	*State Dairymen's Association*
JAMES M. BARTLETT	*Members of the Station Staff*
FREMONT L. RUSSELL	
EDITH M. PATCH	
WARNER J. MORSE	
RAYMOND PEARL	
HERMAN H. HANSON	
FRANK M. SURFACE	
CHARLES E. LEWIS	

THE STATION STAFF.

CHARLES D. WOODS		*Director*
BIOLOGY	RAYMOND PEARL	*Biologist*
	FRANK M. SURFACE	*Associate*
	FREMONT L. RUSSELL	*Assistant*
	MAYNIE R. CURTIS	*Assistant*
	WALTER ANDERSON	*Poultryman*
	LOTTIE E. McPHETERS	*Computer*
CHEMISTRY	JAMES M. BARTLETT	*Chemist*
	HERMAN H. HANSON	*Associate*
	JOANNA C. COLCORD	*Assistant*
	JOSEPH F. MERRILL	*Assistant*
	REX C. GELLERSON	*Inspector*
ENTOMOLOGY	EDITH M. PATCH	*Entomologist*
	ALICE W. AVERILL	*Laboratory Assistant*
PLANT PATHOLOGY	WARNER J. MORSE	*Pathologist*
	CHARLES E. LEWIS	*Associate*
	FRANK D. STERRY	*Laboratory Assistant*
ROYDON L. HAMMOND		*Seed Analyst and Photographer*
ANNIE M. SNOW		*Clerk and Stenographer to the Director*
BLANCHE F. POOLER		*Stenographer*
HENRY A. MILLETT		*Meteorological Observer and Janitor*

BULLETIN No. 166.

DATA ON THE INHERITANCE OF FECUNDITY OBTAINED FROM THE RECORDS OF EGG PRODUCTION OF THE DAUGHTERS OF "200-EGG" HENS.*

Raymond Pearl and Frank M. Surface.

In 1907 the experiment of the Station in breeding Barred Plymouth Rocks for high egg production which had been going on since 1898 came formally to an end. There was planned for 1908 a new experiment designed to test from another standpoint the conclusions which had been tentatively reached from the earlier experiment. It had been noted, though never particularly discussed in the bulletins describing the breeding work of the Station, that the daughters of the so-called "registered hens (namely hens that had produced 200 or more eggs each in the pullet year) did not usually make high egg records. The "200-egg" birds which made up the "registered" flock came in most instances from "unregistered" mothers. It seemed desirable to determine exactly what would be the egg production of the daughters of "200-egg" hens, when these daughters were accorded the same treatment as is given to other pullets. Accordingly the Director of the Station and the late Professor G. M. Gowell outlined an experiment to test this point. The plan of the experiment was as follows: To hatch in the spring of 1907 as many pullets as possible from "200-egg" hens and keep an exact pedigree record on the mother's side of each of these chickens. An exact pedigree record of the male ancestry

---

* Papers from the Biological Laboratory of the Maine Agricultural Experiment Station. No. 10.

This paper forms No. II of a series of "Studies on the Physiology of Reproduction in the Domestic Fowl." No. I of the series has the subtitle "Regulation in the Morphogenetic Activity of the Oviduct" and is published in the Journal of Experimental Zoology. Vol. 6.

was not kept. All male birds used, however, were so-called "registered" cockerels. They were cockerels in whose ancestry the females for at least seven generations had been birds laying 200 or more eggs in the pullet year. These "registered" pullets were then to be housed and fed exactly in the same manner as were the "unregistered" * pullets. The experiment as planned was begun by Professor Gowell and carried on by him until the time of his resignation from the Station in December, 1907. The continuation of the experiment was turned over to the department of biology along with the other poultry work. It is the purpose of this bulletin to report the results of this experiment.

The specific questions which this experiment was instituted to answer may be briefly stated as follows:

1. Will the daughters of high laying hens ("200-egg" birds) on the average produce more eggs in a given time unit than will birds of less closely selected ancestry?

2. What data do the performance records of such selected birds afford regarding the inheritance of egg producing ability in the domestic fowl?

PLAN OF THE EXPERIMENT.

On the first of November, 1907, there were put into House No. 2 of the Station's plant, 250 pullets. Each of these was the daughter of a hen that had laid approximately 200 eggs in her pullet year. These 250 pullets were divided into flocks of 50 each and were fed and handled in every way exactly in accordance with the usual methods of the Station (cf. Bulletin No. 144). They were an even lot of birds and had the strong, vigorous appearance which has characterized the Station's Barred Plymouth Rock stock. They were to the eye slightly small for Barred Plymouth Rocks, and also gave the general impression of being slightly smaller than the "unregistered" pullets of the same age in the other houses. The smaller size of the "registered" pullets had been noted for some years in the breeding work of the Station.

At the same time that these 250 "registered" pullets (so-called because from "registered" mothers) were put into the house

* That is, birds of similar breeding except that their mothers laid from 150 to 200 eggs each in their pullet years instead of over 200 eggs.

there were also put in 600 other Barred Plymouth Rock pullets. These were of the same average age as the 250 "registered" birds and differed in their breeding only in respect to their mothers. They came from hens that had laid less than 200 eggs during the pullet year and more than 150. "Registered" cockerels (from the "200 egg line") were used as the male parents for all the pullets both "registered" and "unregistered." The 600 "unregistered" birds were divided into flocks as follows: Two flocks of 50 birds each were kept in two pens in House No. 2 exactly like the pens in which the "registered" birds were kept. The remaining 500 birds were divided into four flocks—two of 100 birds each and two of 150 birds each and housed in the four pens of House No. 3. These pens are essentially like those of House No. 2, differing chiefly in the matter of size.

The birds used in this experiment whether "registered" or "unregistered" were not closely inbred. In the breeding work of the Station for many years Professor Gowell exercised the greatest care to avoid close inbreeding, which he felt to be wrong in theory and dangerous in practice. The breeding practiced was what is known as "line-breeding." The important point for the present discussion lies in the fact that the "registered" ("200-egg") birds were, on the average, neither more nor less closely inbred than the "unregistered" birds. "Registered" and "unregistered" were alike in this regard.

Except in the matter of flock size the treatment and management of all the birds whether "registered" or "unregistered" was exactly the same. All were given the same feed and care in every way.

All the birds were trap nested from November 1, 1907, to July 1, 1908. The trap nest records were stopped at the latter date owing to the necessity of giving the poultry houses a thorough overhauling and renovating. The records obtained, however, cover the major portion of the year and just that portion which is of most interest and significance in the study of egg production.

COMPARISON OF THE EGG RECORDS OF MOTHERS AND DAUGHTERS.

In undertaking a discussion of the results of the experiment which has been outlined the proper starting point obviously is

the egg production and other characteristics of the mothers which produced the 250 so-called "registered" pullets. Then the egg production of each mother's progeny may be compared with her own production. The significant data on this matter are shown in Table I. This table gives in the first column the band number of each "registered" mother hen known to have one or more daughters among the 250 pullets. The second column of the table shows the number of eggs produced by each of these mother hens between November 1 of her pullet year and November 1 of the following year. The third, fourth and fifth columns of the table show the number of daughters which each of these mother hens had among the 250 birds. The first of these columns gives the *total* number of daughters for each mother. The second column (rubric "Nov.-Mar.") gives the number of daughters of each mother which survived to March 1, 1908. The third column gives the number of daughters surviving until June 1, 1908.

The sixth column of the table shows the number of eggs laid by each of the registered mother hens in the experiment between November 1 and March 1 of her pullet year. In other words, this column gives the individual mother's *winter* egg record. The seventh column gives the corresponding figures for the daughters. In this column there is set down the average egg production between November 1 and March 1 of the pullet year of the daughters of each individual mother. For example, it appears from the first line of the table that the 12 daughters of mother hen No. 7 averaged to lay between November 1 and March 1, 14.83 eggs each, while in the corresponding period of her own life hen No. 7 laid 33 eggs. The eighth column of the table gives the egg record of each mother hen between March 1 and June 1 of the pullet year. Finally, the last column of the table gives the corresponding figures for the daughters. In this column are the averages between March 1 and June 1 of each group of daughters coming from a particular mother.

TABLE I.

Showing the Egg Records of the "Registered" Hens and the Number and Egg Records of Their Daughters.

Band number of "registered mother" hen.	Mother's egg production from Nov. 1 of pullet year to Nov. 1 of following year.	Number of daughters of each "registered" hen in the experiment.			Winter egg production. Nov. 1—Mar. 1.		Spring egg production. Mar. 1—June 1.	
		Total.	Nov. 1–Mar. 1	Mar. 1–June 1	Mother's.	Daughter's average.	Mother's.	Daughter's average.
7	193	12	12	12	33	14.83	81	47.75
33	192	8	8	8	30	13.37	68	53.25
578	196	4	4	4	42	23.75	59	42.25
253	200	9	8	7	65	23.87	45	38.14
46	184	3	3	3	64	15.33	56	51.00
460	208	8	8	8	61	15.50	60	44.87
617	183	4	4	4	47	15.25	56	38.00
42	216	7	7	6	46	13.28	67	52.83
169	210	17	15	15	70	13.47	54	44.43
150	193	5	5	5	56	18.00	53	50.80
236	180	7	6	5	24	20.83	62	46.20
152	200	6	6	6	49	18.83	69	43.33
105	217	8	8	8	68	17.25	66	48.12
386	203	9	9	9	55	4.88	59	40.88
911	196	3	3	3	52	27.33	62	55.33
510	212	3	3	2	69	0.00	59	12.50
404	203	2	2	2	55	19.50	56	62.00
174	208	6	6	6	43	24.00	68	44.16
166	221	7	7	7	66	7.14	56	46.57
2	190	10	10	10	48	17.90	60	45.80
505	204	6	6	5	58	17.66	43	38.00
464	202	7	7	7	77	19.57	62	51.28
32	203	9	9	9	64	11.00	55	50.33
111	?	10	—	—	—	—	—	—
379	203	4	4	4	63	24.25	60	47.50
130	208	3	3	3	68	14.00	51	53.00
49	200	4	4	3	29	18.00	65	42.33
351	201	5	5	5	68	15.20	49	53.80
9	186	8	7	7	60	14.14	49	59.85
614	?	9	—	—	—	—	—	—
14	197	6	5	4	66	2.40	68	47.75
349	203	4	4	3	51	10.25	55	37.33
303	246	4	4	4	83	7.25	60	29.70
Total number of "mothers" represented.	Average "mother's" egg* production.	TOTALS.			Mother's average Nov.—Mar. production.	Daughter's average, Nov.—Mar., production.	Mother's average Mar.—June, production.	Daughter's average Mar.—June, production.
33	201.8	217	192	184	55.80	15.29	59.13	46.61

* Omitting the two birds without records, No. 111 and No. 614.

From this table a number of points are to be noted.

1. In the first place an examination of the totals shows that only 217 out of the 250 pullets supposedly in the experiment are accounted for in the table. The remainder of the 250, namely, 33 birds, do not appear in the table for one or another of the following reasons: Such birds may have lost their leg bands as chickens and hence lost their individual pedigree connection, though still known to be the daughters of *some* 200 egg hen. Or there may have been failure to make any note of the chick bands originally put on. In dealing with the results of the experiment it has been deemed wisest to leave all pullets not having definite pedigree records out of account.

2. It is further to be noted that two of the mother hens—Nos. 111 and 614—have an interrogation mark in the column devoted to the mother's egg records. The reason for this omission lies in the fact that in the past egg records of the Station there are two birds recorded as each having a band number 111 and also laying over 200 eggs, and there are two birds each having a band number 614, and each recorded as having laid over 200 eggs. There is nothing in the records of the present experiment, or in the memory of those who had the details of the work in hand to tell which of these duplicate birds were the ones actually used in this work. Consequently, it is impossible to insert in the table any egg record for them. It is certain, however, that they were both in the "registered" class.

3. Another point which needs discussion is that not all the mother birds laid 200 eggs or over between November 1 of their pullet year and November 1 of the following year. In looking through the records of the mothers whose band numbers are entered in the first column of the table it was found that they fell into three classes, as follows: (a) Those birds that laid 200 or more eggs between November 1 of their pullet year and November 1 of the following year. (b) Birds that laid 200 eggs in a year (365 days) forward from the day on which they laid their first egg. (c) Birds which neither laid 200 eggs between November 1 and November 1, nor in the year forward from the date of their first laying, but which only fell a few eggs short of doing one or the other of these two things. Such

birds were apparently included at the beginning of the experiment as "registered" hens "by courtesy." *

4. It will be seen from the totals of the table that 33 mother birds produced 217 pullets. This is at the average rate of 6.6 pullets per mother. If it be assumed that the sex ratio in fowls is approximately equal to unity or, in other words, that males are as likely to be produced as females, this means that the average production of viable offspring per mother for these registered hens during the breeding season was 13.2 birds. No record was kept to show how many eggs were involved in the production of these birds.

5. The average egg production of the mothers omitting the two birds (Nos. 111 and 614) which have no record is 201.8 eggs per bird. This average indicates that the non-uniformity of mothers described in paragraph 3 above does not in any essential way affect the point of the experiment. The birds used as mothers, all taken together, averaged slightly more than 200 eggs apiece in their pullet years. Transferring to relative figures * it appears that the mother's average egg production for the year was 55.3 per cent,† $(201.8 \times 100) \div 365$.

6. Turning now from a consideration of the mothers' gross total records to the records made in particular seasons of the year it is seen that the registered mother hens involved in the experiment averaged to lay 55.80 eggs per bird between November 1 and March 1 of the pullet year. This is, of course, an excellent winter egg record. Transferring from absolute to relative figures it is found that 55.80 eggs between November 1 and March 1 correspond to a percentage egg production of 46.5 per cent. It will be noted that this is a lower percentage record than that of these same birds in their total yearly production (55.3 per cent from paragraph 5 above).

7. The egg production of the registered mother hens in the spring months (March 1 to June 1) is seen to average 59.13

---

* It will be recalled (cf. p. 49 supra) that this experiment had been under way 8 months before the writers of this bulletin took charge of it. They therefore cannot be held responsible for the points noted in paragraphs 1, 2 and 3.

* According to the rule given in Me. Agr. Exp. Sta. Bulletin No. 165.

† This figure is of some interest as indicating what a *relatively* small proportion of the theoretically maximum character is being selected to, when 200 eggs birds are bred.

eggs per bird. This figure corresponds to a percentage egg production during the same period of 64.4 per cent. This is nearly a 20 per cent higher production proportionately than that of the winter months. It shows in a very striking way that even with record layers such as these hens were the egg production is markedly increased in the spring months (the natural mating and laying season) as compared with the winter months. It will be further noted that the spring percentage production is about as much above the percentage production of the same birds throughout the whole year as the winter production is below this figure.

8. Turning now to the production of the daughters of these "registered" birds in corresponding periods of their pullet years very different results are obtained. Taking first the winter production, it is seen that the 192 daughters whose records can be included averaged to produce between November 1 and March 1 of their pullet years only 15.29 eggs per bird. This absolute production corresponds to a relative or percentage production of 12.7 per cent for the same period. It is evident that the daughters do not belong in anything like the same class as the mothers as winter egg producers. The mothers' average production for the corresponding period of their pullet year was nearly 4 times as great as the daughters'. (Exactly $46.5 \div 12.7 = 3.7$). This great reduction of the daughters' average winter production below the mothers' is most striking and unexpected. It is to be expected on general grounds that there would be some regression, but so much as this would hardly be anticipated.

9. From the last column of the table it is seen that the daughters' laying during the spring months averaged to be 46.61 eggs per bird. This corresponds to a relative or percentage egg production of 50.7 per cent. It is evident that this is a relatively very much better egg production than is that of the daughters during the winter months. It still, however, is nearly 15 per cent below the mothers' egg production in the corresponding part of the year. The fact that the spring months are the natural laying season for fowls shows itself in these daughter records even more strikingly than in the records of the mothers. The daughters' spring production (*their best*) is still,

however, roughly 5 per cent lower than is the mothers' total relative yearly production (paragraph 6).

10. From the data discussed in paragraphs 6 to 9 the fact appears that the daughters' gain in spring as compared with winter egg production is proportionately much greater than the mothers' similar gain. Thus, the daughters' relative egg production is 38.0 per cent higher in the spring months than it is in the winter months, whereas the mothers' relative spring production is only 17.9 per cent higher than their winter production. The daughters gained more than twice as much as the mothers. This of course finds its explanation in the fact that the winter production of the mothers was so much better than that of the daughters that the mothers could not possibly make so great a relative gain in spring as compared with winter laying. Their winter laying was already too high. The daughters had a poor winter record and hence had no difficulty in making a relatively high gain in the spring production.

11. The general conclusion to be reached from the data set forth in Table II is clearly, so far as these data indicate, that the daughters of "200-egg" hens when kept under substantially the same conditions and treated in the same way as their mothers, are markedly inferior to them in winter and in spring egg production.

This result inevitably raises the question: Did "like produce like" in this experiment? The assumption made in much of the practical breeding of poultry is that if one wants to get good winter layers he needs only to breed from good winter layers. But in this experiment there is found no evidence whatever that the good winter layer produced the good winter layer. In fact, taking the data as a whole, exactly the contrary is the case. The mothers on the average were wonderfully good winter layers. The daughters, on the other hand, were extremely poor winter layers. These, be it remembered, are statements of fact, not of theory.

One must be very cautious about drawing the conclusion from the data set forth that there is no inheritance of fecundity from parent to offspring in the domestic fowl. There are many further points which must be taken into account before any conclusion whatever as to the inheritance of fecundity may be certainly reached. The remainder of this bulletin will be

devoted to a discussion of some of these further factors which enter into the problem. The aim so far has been to set forth in as clear and unequivocal manner as possible, the definite fact that in the Station's experience thus far the daughter of a "200-egg" hen is, on the average, an exceptionally poor winter layer, instead of an exceptionally good one.

THE PERIOD COVERED BY THE RECORDS.

The first question which naturally suggests itself in connection with the data which have been presented in the Table I is as to whether it is not conceivable that different results might have been obtained had the experiment been continued for a longer time so that the daughters could have made egg records covering a longer period of their lives. In other words, it might conceivably be maintained that if the daughters' records for the whole pullet year had been compared with the mothers' records for the same period of their lives there would not have been so great a discrepancy between the averages of the two groups. It was necessary, on account of making changes in the buildings of the poultry plant to stop the trap nest records on June 30, 1908. There are then lacking records of four months (July, August, September and October) egg production of the daughters' pullet year. These are the four least important months of all, however, from the standpoint of the practical study of egg production.* We can get light on the significance of the contention that different results might have been obtained in this experiment had the daughters' records covered the whole year in two ways.

(1) The average egg production of the mothers from November 1 to June 1 of their pullet year was in round numbers 114.9 eggs per bird. Since the average total production of the mothers for the whole year was 201.8 eggs per bird it, of course, follows that their average production from June 1 to November 1 was 86.9 eggs per bird. Now the daughters' egg production from November 1 to June 1 in their pullet year was, as has been seen, 61.9 eggs per bird. If it be assumed that after June 1 the daughters would have laid on the average just as well during the remainder of the year as did the group

* See the discussion on this point in Me. Agr. Exp. Sta. Bulletin No. 165.

of mothers what would have been the average egg production of the daughters for the whole year? This can be determined by adding 86.9, the mothers' average production from June 1 to November 1, to 61.9, the daughters' production from November 1 to June 1. In this way one gets 148.8 eggs as the average production of the daughters for the whole year, had they been allowed to make a record for the year and assumed to lay as well as the mothers during the summer and fall months.

In considering this result two things must be kept in mind. In the first place the assumption that if the daughters had been allowed to continue their records they would have laid on the average as well as the mothers during the summer months is, from the standpoint of actual experience, an absurd one. This is probably sufficiently evident on general grounds, but we further have definite mathematical evidence of it. It is not possible to take space to present this evidence in detail here, but in a word it consists in the fact that the egg production at any one part of the year has been found to be positively correlated with that of any other part of the year. That is, it has been found on the basis of the 9 years trap nest records at this Station that on the average the bird which is an unusually good layer at one period of the year will also have an unusually good egg production record for any other portion of the year whatsoever and vice versa. The poor winter layer does not on the average, and in the long run make the good summer layer, though this is often assumed to be the case.

In the second place it is clear enough that, even if the truth of the assumption that the daughters would have laid as well as the mothers during the summer could be granted, the daughters' average would still be more than 50 eggs lower for the year than the mothers'. No further comment on this point seems necessary.

(2) So far there have been considered only the results when the records are broken up into winter and spring laying periods. It is perhaps well to examine the figures for the whole period over which we have data, namely, from November 1 to July 1 of the pullet year. Comparing mothers and daughters in regard to egg production over this period (two-thirds of the year) we have the results shown in Table II.

TABLE II.

Average Egg Production of "200-egg" Hens and Their Daughters. November 1 to July 1.

Character.	Value.
Number of mothers completing records	31
Number of pedigreed daughters completing records	180
Mother's absolute average egg production, Nov. 1—July 1	135.13
Daughter's " " " " " 1 " 1	74.47
Mother's relative " " " " 1 " 1	55.8%
Daughter's " " " " " 1 " 1	30.8%

The figures in this table for the longer period simply confirm and make more emphatic the results obtained with the shorter periods discussed in Table I. Lengthening the period of record does not bring mothers' and daughters' averages any nearer together. There is no reason whatever to suppose that these averages would have been any nearer together if records for the daughters had been taken for the whole year.

TESTS OF THE INHERITANCE OF FECUNDITY.

There are two other points which must always be considered in discussing the inheritance of egg production besides the comparison of the daughters' average egg production with that of their mothers. In the first place it is quite conceivable that the daughters' average production might be very much lower than their mothers' average production and there still be inheritance of the egg producing ability. This seeming paradox might arise in this way. If unfavorable environmental influences acted in the case of daughters the average production of the whole group of daughters might be considerably below that of the mothers. At the same time the exceptional mother (that is the mother whose production was above the average for *mothers*) might produce the exceptional daughter (the daughter whose performance was above the average for *daughters*). Such a condition of affairs would obviously indicate the inheritance of egg producing ability and yet clearly might exist quite independently of the relative magnitude of the averages of the mother and daughter groups as wholes.

To determine whether there is such an inheritance of egg producing ability independent of the group averages it is neces-

sary that the *correlation* between mothers and daughters in respect to egg production be actually measured. From such measurement it can be told whether on the average the exceptional mother produces the exceptional daughter or whether the exceptional daughter is as likely as not to be the daughter of the mediocre or poor mother.

In the second place if the results of an experiment in which the mothers are especially selected are to be used in the discussion of inheritance of egg producing ability it is necessary that the daughters' average production be compared not merely with the mothers' average, but also with the average of other birds of the same age as the daughters and kept under the same environmental conditions but not of selected ancestry.

THE CORRELATION BETWEEN MOTHERS AND DAUGHTERS IN RESPECT TO EGG PRODUCTION.

Taking up first the question of the correlation between the egg production of the mothers and the daughters it is necessary to answer the following question. Did the exceptionally good mother in this experiment on the average produce daughters above the average of daughters or not? Some general indication as to the answer which the data give to this question is afforded in Figs. 10 and 11. The plan on which these figures are constructed is as follows: The upper of the two horizontal zigzag lines in each figure represents the egg production of the 31 mothers included in the experiment. This upper zigzag line in Fig. 10 is the graph of the data given in the sixth column of Table I. The lower zigzag line in each figure is the graph of the average egg production of each of the groups of daughters associated with the 31 mothers. In Fig. 10 the lower zigzag line is the graph of the data given in the seventh column of Table I. In general any plotted point in the upper of the two zigzag lines shows the mother's performance during a given period of the year and the plotted point directly below it on the lower zigzag line shows the average performance of this mother's daughters.

Fig. 10 gives the data for the winter (November 1 to March 1) egg production and Fig. 11 the spring (March 1 to June 1) egg production.

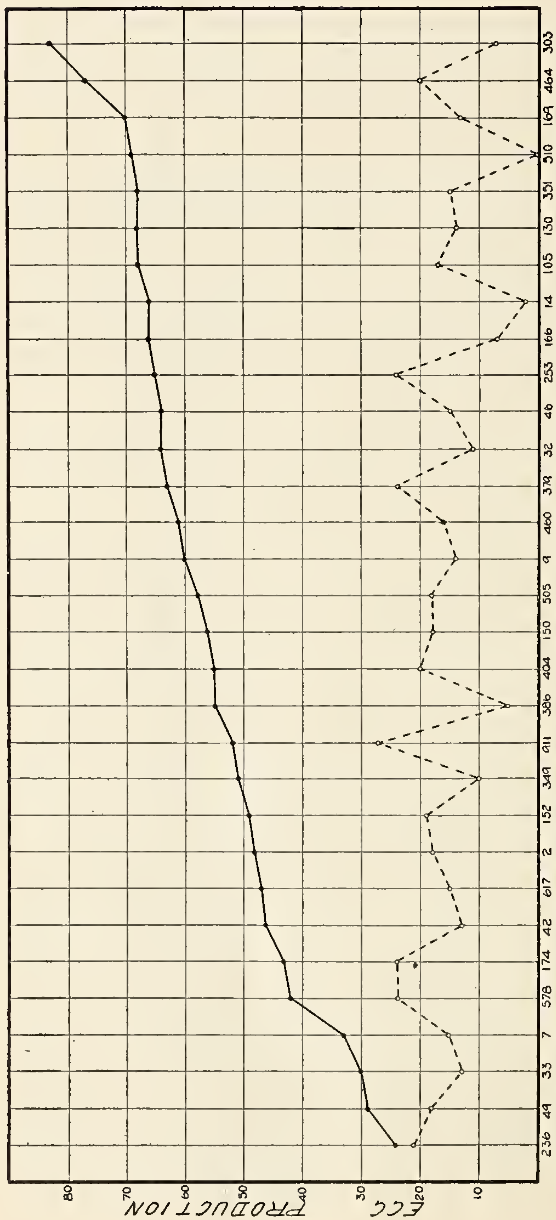

Fig. 10. Diagram showing the relation between "200-egg" hens and their daughters in regard to *winter* (November 1 to March 1) egg production. The solid line and black circles give the mother's production; the broken line and open circles the daughters' averages. Data from Table I. The figures along the bottom of the diagram are the mothers' band numbers.

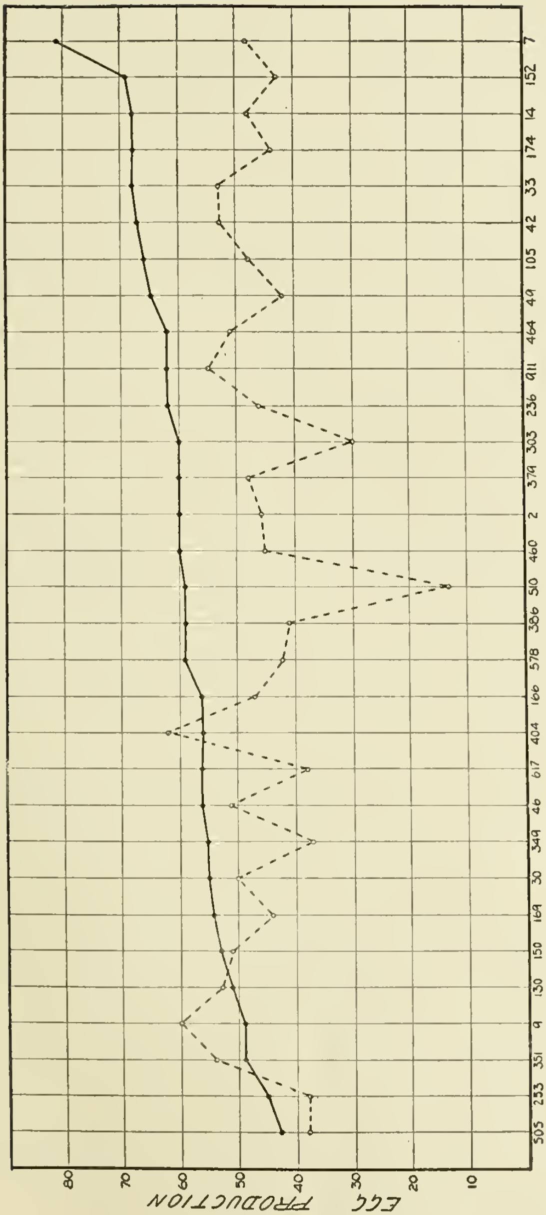

Fig. 11. Diagram showing the relation between "200-egg" hens and their daughters in regard to *spring* (March 1 to June 1) egg production. Significance of lines and figures as in Fig. 10.

If, on the average, the exceptionally good mother produced the exceptionally good daughters, and the exceptionally poor mother the exceptionally poor daughters it would be expected that the two lines in each of these two figures would run, in the main, parallel to each other. No such a parallelism is apparent, however. The two lines in each of the figures zigzag up and down in a manner quite independent of each other. The daughters' line is as liable to go up when the mothers' line is going down as to do the opposite. These diagrams clearly do not give any evidence that egg producing ability was inherited in this experiment.

Resort must be had, however, to a more exact appreciation of the correlation between mothers and daughters in respect to egg production. Such correlation may be accurately measured by proper mathematical methods. It is not necessary to enter into a discussion of these methods at this place.*

In general the procedure is as follows: A statistical table known as a "correlation table" is made showing the egg production of each individual daughter and each individual mother. From this table is calculated the so-called "coefficient of correlation" which measures the average degree of association between mother and daughter in respect to the character under discussion. This coefficient of correlation is of such character that it may take values only between the limits of zero and 1. When the correlation coefficient is equal to zero it means that there is absolutely no association or correlation between the characters under discussion. That is to say, in the present case a correlation coefficient of zero would mean that an exception-

---

* Descriptions of modern biometrical methods may be found in any of the following works:

1. Pearson, K. Grammar of Science. Second edition. London (A. & C. Black) 1900. Pp. xviii+548.
2. Elderton, W. P. Frequency Curves and Correlation. London (Layton) 1907. Pp. xiii+172.
3. Davenport, C. B. Statistical Methods with Special Reference to Biological Variation. Second edition. New York (J. Wiley & Sons) 1904. Pp. viii+223.
4. Davenport, E. The Principles of Breeding. Boston (Ginn & Co.) 1907. Pp. xiii+727.
5. Davenport, E. and Rietz, H. L. Type and Variability in Corn. Ill. Agric. Exp. Sta. Bulletin No. 119, pp. 1-38. 1907.

ally high producing mother is, on the average, as likely to produce exceptionally poor as exceptionally high producing daughters and *vice versa*. On the other hand a correlation coefficient of 1 means a perfect association or correlation. In the present case a correlation coefficient of +1 would indicate that an exceptionally good mother always and invariably produced an exceptionally good daughter which was, as compared with daughters in general, exactly as exceptional relatively as the mother was as compared with other mothers. As the correlation coefficient takes different values between zero and one it indicates varying degrees of association or correlation between the characters under consideration.

There are several different ways in which the problem of the correlation between mother and daughter in respect to egg production may be approached. In the first place it is possible to make a table in which each daughter and her mother shall be individually entered. From such a table the correlation between mother and daughter in respect to egg production can be measured. It is obvious, however, that this procedure weights each mother with her own fecundity. This arises from the fact that while each individual daughter has an individual mother there are not as many individual mothers as there are daughters. If a mother produces six daughters she will appear six times in the table with whatever egg record she may have made. The mother with only three daughters will have her egg record appear only three times in the table and so on. In general, the mother's egg record by this procedure will be weighted according to the number of daughters which she had in the experiment. It is apparent that this method is not a perfect one, but it is the only practicable way of dealing with ordinary statistics of fecundity yet devised which enters every individual offspring separately in the correlation table. It is a method which has been used by Pearson * (though not exclusively) in the study of the inheritance of fecundity in race horses and of fertility in man. To be entirely fair it would be necessary in

* Cf. Pearson, K., Lee A., and Bramley-Moore, L. Mathematical Contributions to the Theory of Evolution. VI—Genetic (Reproductive) Selection: Inheritance of Fertility in Man and of Fecundity in Thoroughbred Racehorses. Phil. Trans. Roy. Soc. Vol. 192A, pp. 257-330. 1899.

determining the degree of inheritance of fecundity in this way, to use only families in which the number of daughters were equal so that each mother's record would be equally weighted.

Another possible way of approaching the problem is to enter in the correlation tables only one daughter for each mother. This gets around the weighting of the mothers with their own fecundity but only by involving the further difficulty which arises from the existence of individuality amongst the daughters. This difficulty is easily illustrated. Suppose, in the concrete case under discussion, that some particular mother hen has nine daughters, which one of these daughters shall be taken as the one to have its record entered in the correlation table with the mother's? It is, of course, obvious that, in advance of special investigations of the degree of individuality among daughters in general in regard to egg production, it will be possible to get quite different results from the inheritance of fecundity according as one picks and chooses the individual daughter to enter into the table by this method.

On the whole the element of error introduced by weighting mothers with their own fecundity appears to us likely to be less than the error arising from choosing single individual daughters as representative of their families. In view of this consideration and of the further fact that this is the method which has been quite generally adopted by students of the inheritance of fecundity it has been decided in the present case to make correlation tables of the sort wherein all daughters (and their mothers) are entered as a first point of approach to the problem. Such correlation tables for measuring the inheritance of egg production are given in Tables III, IV and V. Of these tables No. III deals with winter (November 1 to March 1) egg production. No. IV with spring (March 1 to June 1) egg production and No. V with the total (November 1 to July 1) egg production.

It is desirable, for the benefit of those not accustomed to tables of double entry such as these are, to explain and illustrate how such tables are to be read. The figures in the body of the table in each case denote the frequency of occurrence of the pair of events indicated by the marginal classes. To take a concrete illustration from Table III, it will be noted that in the first row and eighth column of the body of the table there is an entry "5."

TABLE III.

Showing the Correlation Between "Registered" Pullets and Their Mothers in Respect to Winter (November 1 to March 1) Egg Production.

	Mother's Egg Production.															
Daughter's Egg Production.	24–27.9	28–31.9	32–35.9	36–39.9	40–43.9	44–47.9	48–51.9	52–55.9	56–59.9	60–63.9	64–67.9	68–71.9	72–75.9	76–79.9	80–83.9	Totals.
0–3.9	1	3	2	–	1	3	7	5	3	5	12	8	–	1	1	52
4–7.9	–	3	2	–	1	2	2	3	3	3	3	8	–	2	1	33
8–11.9	1	3	1	–	–	1	1	–	–	2	5	6	–	–	1	21
12–15.9	–	1	2	–	3	2	–	1	1	1	4	1	–	1	1	18
16–19.9	1	–	3	–	–	–	3	1	1	1	–	4	–	–	–	14
20–23.9	–	–	1	–	1	–	1	2	1	1	3	–	–	–	–	10
24–27.9	–	–	–	–	–	1	1	1	–	2	–	1	–	–	–	6
28–31.9	1	–	–	–	1	–	2	–	–	1	1	1	–	1	–	8
32–35.9	2	–	–	–	–	–	–	–	–	–	1	3	–	–	–	6
36–39.9	–	–	–	–	1	1	–	–	–	–	1	–	–	1	–	4
40–43.9	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
44–47.9	–	–	–	–	–	–	1	1	–	1	1	–	–	1	–	5
48–51.9	–	–	1	–	1	1	–	–	–	1	–	–	–	–	–	4
52–55.9	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	2
56–59.9	–	2	–	–	1	–	1	–	2	–	–	–	–	–	–	6
60–63.9	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
64–67.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
68–71.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
72–75.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
76–79.9	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Totals......	6	12	12	0	10	11	20	14	11	19	32	34	0	7	4	192

This signifies that in the experiment there were five pullets whose own egg records for the winter period fell between 0 and 3 eggs inclusive, and whose mothers' egg records for the corresponding period of their pullet years were from 52 to 56 eggs inclusive. To take another example, it will be seen from Table V that there were three daughters whose total production from November 1 to July 1 fell between 85 and 89 eggs inclusive, and whose mothers' egg production in a corresponding period of time fell between the figures 155 and 159 inclusive. These

examples will make clear how the tables in general are to be read.

Another possible way of getting at the correlation between mothers and daughters in respect to egg producing ability is to correlate the mother's performance with the *average* performance of her daughters. This method of procedure in a measure gets over both of the difficulties which have been noted above. In the first place the mothers are not weighted with their fecundity. In the second place, since the *average* daughters' performance is taken, undue weight is not given to the factor of individuality among the several daughters. It has seemed desirable

TABLE IV.

Showing the Correlation Between "Registered" Pullets and Their Mothers in Respect to Spring (March 1 to June 1) Egg Production.

		Mother's Egg Production.											
		40–43.9	44–47.9	48–51.9	52–55.9	56–59.9	60–63.9	64–67.9	68–71.9	72–75.9	76–79.9	80–83.9	Totals.
Daughter's Egg Production.	0–3.9	–	–	–	2	2	3	–	–	–	–	–	7
	4–7.9	–	–	–	–	1	1	–	–	–	–	1	3
	8–11.9	–	–	–	1	1	–	–	–	–	–	–	2
	12–15.9	–	–	–	–	1	–	–	–	–	–	–	1
	16–19.9	–	–	–	1	2	1	2	1	–	–	–	7
	20–23.9	–	–	–	–	2	1	–	1	–	–	1	5
	24–27.9	1	–	–	2	1	–	1	–	–	–	–	5
	28–31.9	1	–	1	1	1	2	–	1	–	–	1	8
	32–35.9	1	–	–	2	2	3	1	2	–	–	–	11
	36–39.9	–	–	–	1	2	–	1	2	–	–	–	6
	40–43.9	1	–	1	2	–	2	–	2	–	–	1	9
	44–47.9	–	–	1	2	4	5	–	1	–	–	1	14
	48–51.9	–	–	–	2	4	3	1	–	–	–	3	13
	52–55.9	–	–	3	2	4	7	3	6	–	–	–	25
	56–59.9	–	–	1	4	3	1	2	5	–	–	–	16
	60–63.9	1	–	4	7	2	5	5	1	–	–	–	25
	64–67.9	–	–	4	2	5	5	1	–	–	–	1	18
	68–71.9	–	–	–	1	–	1	–	1	–	–	1	4
	72–75.9	–	–	–	1	–	–	–	1	–	–	2	4
	76–79.9	–	–	–	–	–	1	–	–	–	–	–	1
Totals..........		5	0	15	33	37	41	17	24	0	0	12	184

TABLE V.

Showing the Correlation Between "Registered" Pullets and Their Mothers in Respect to Total (November 1 to July 1) Egg Production.

Mother's Egg Production.	Daughter's Egg Production. 0–4.9	5–9.9	10–14.9	15–19.9	20–24.9	25–29.9	30–34.9	35–39.9	40–44.9	45–49.9	50–54.9	55–59.9	60–64.9	65–69.9	70–74.9	75–79.9	80–84.9	85–89.9	90–94.9	95–99.9	100–104.9	105–109.9	110–114.9	115–119.9	120–124.9	Totals.
105–109.9	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	1	–	1	–	–	5
110–114.9	–	–	–	–	–	–	–	–	–	1	–	–	1	2	1	–	–	–	–	–	3	–	–	–	–	8
115–119.9	–	–	–	–	–	1	–	1	–	–	1	–	1	–	1	–	1	–	–	–	–	1	–	–	–	7
120–124.9	–	1	–	–	1	–	1	–	–	–	–	–	–	1	2	1	3	3	2	5	–	–	2	–	–	22
125–129.9	1	–	–	–	–	–	–	–	–	–	1	1	–	2	–	1	–	2	–	2	1	1	–	–	–	12
130–134.9	–	–	–	–	1	1	1	1	–	–	1	1	–	1	4	5	–	–	1	–	–	–	1	–	–	18
135–139.9	–	1	–	–	–	–	–	–	1	1	–	1	–	–	–	2	4	2	2	4	2	1	–	–	–	21
140–144.9	1	–	–	–	4	1	1	–	1	3	–	1	2	6	4	2	5	6	5	5	4	–	1	1	1	54
145–149.9	1	–	–	–	–	–	–	–	–	2	–	–	1	3	–	3	2	–	1	–	–	–	1	–	–	14
150–154.9	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	1	4	–	–	–	–	1	–	–	–	8
155–159.9	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	3	–	1	–	–	1	–	–	7
160–164.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0
165–169.9	1	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	4
Totals........	5	2	0	0	6	4	3	2	2	7	5	5	6	16	12	15	20	16	11	19	11	4	7	1	1	180

to make a study of the correlation between the mother's individual performance and the daughter's average performance for each of the egg laying periods here under discussion, in order to compare the results so obtained with the results which one gets by the more usual method of allowing the mothers' records to be weighted with their fecundity. In determining the degree of correlation in this way it is neither necessary nor desirable in the present case where we are dealing with such small numbers (31 mothers only) to make a correlation table for the evaluation of the coefficient. Instead the correlation coefficient may most accurately be determined directly from the data given in Table I without grouping.

Besides the evidence as to the inheritance of egg producing ability afforded by the coefficient of correlation between mother and daughter in respect to this character, light may also be obtained on the problem from the relative values of constants measuring variability in egg production. It is a fundamental principle of breeding by selection that the offspring of selected parents will be less variable than the offspring of unselected parents, or, in other words, than the general population. It is to be expected that following selection there will be a reduction in variability. Selection is made to a type and if a line of breeding is successful it is justifiable to assume that the offspring after selection will conform more closely to the type than did the individuals before selection. It is, on this account, important in all discussions regarding the inheritance of a character to determine the variability of that character following selection. In the present case the variation can be measured by well known and accurate methods in connection with the mathematical processes involved in determining the correlation coefficients. The variation constants will be tabled with the correlation coefficients.

The constants of variation and correlation measuring the degree of inheritance in egg production exhibited in this experiment are shown in Table VI. These constants have been determined from the data given in Tables I, III, IV, and V.

TABLE VI.

Constants Measuring the Degree of Inheritance in Egg Production. "200-Egg" Hens and Their Daughters. Experiment of 1907-1908.

SUBJECT.	Standard deviation.*	Coefficient of variation.*	Coefficient of correlation.
Variation in winter (Nov. 1—Mar. 1) egg production. *Mothers* unweighted. (Table I)..	14.06±1.20	25.20±2.29	-
Variation in spring (Mar. 1—June 1) egg production. *Mothers* unweighted. (Table I)..	7.73±.66	13.07±1.13	-
Variation in winter egg production. *Mothers* weighted with their fecundity. (Table III)	14.93±.51	26.57±.97	-
Variation in spring egg production. *Mothers* weighted with their fecundity. (Table IV)	8.41±.30	13.80±.49	-
Variation in total** (Nov. 1—July 1) egg production. *Mothers* weighted with their fecundity. (Table V)	12.69±.45	9.32±.33	-
Variation in winter egg production. *Daughters*. (Table III)	16.10±.55	101.14±6.44	-
Variation in spring egg production. *Daughters*. (Table IV)	18.10±.64	38.66±1.54	-
Variation in total egg production. *Daughters*. (Table V)	26.38±.94	35.43±1.41	-
Correlation between mothers and daughters in *winter* egg production. (Table III)	-	-	—0.068±.048
Correlation between mothers and daughters in *spring* egg production. (Table IV)	-	-	+0.023±.050
Correlation between mothers and daughters in *total* egg production. (Table V)	-	-	—0.055±.050
Correlation between the mother's individual *winter* performance and her daughter's average winter performance	-	-	—0.329±.108
Correlation between the mother's individual *spring* performance and her daughter's average spring performance	-	-	+0.034±.121

From this table the following points are to be noted:—

1. Considering first the correlation coefficients at the bottom of the table it is apparent that they give no evidence of a positive correlation between mother and daughter in respect

* These constants are measures of variation. The standard deviation measures variation in absolute units (in the present case, eggs), while the coefficient of variation measures it in relative (percentage) units. The larger each of these constants is the greater the variability denoted in the character under consideration.

** "Total" is here used simply as a convenient verbal label of the whole period covered by the egg records *in this experiment*.

to the egg production during any portion of the year. The coefficients are, with a single exception, not sensibly different from zero. In all three of the cases where the correlation is determined from the tables in which the mothers are weighted with their fecundity the correlation coefficients are not sensibly larger than their probable errors. When the mother's individual performance is correlated with the daughter's average performance the coefficient also is sensibly equal to zero in the case of the spring production.

2. In three out of the five cases the sign of the correlation coefficient is negative. In one of these cases, namely that in which the mother's individual winter performance is correlated with her daughters' average winter performance, the negative coefficient is large enough to be sensible in comparison with its probable error. The meaning of a negative coefficient of correlation is, illustrating from this particular experiment, that the mother with a record *above* the average for mothers in general, produced daughters whose records were on the average *below* those for daughters in general. In other words, the negative coefficient indicates that the relatively high producing mother produced the relatively low producing daughter. As has been said, however, only one of these negative coefficients can, when taken alone, be considered to be significant in comparison with its probable error.

3. Turning to the variation results it is seen that whether the variation is measured absolutely or relatively, the daughters, as would be expected, are much more variable than the mothers. In the case of the coefficient of variation, the daughters are from 3 to 4 times as variable as the mothers in respect to the egg production of corresponding periods of the year. The daughters show a greater variation than the mothers regardless of whether the mothers are weighted with their fecundity. The daughters' variability clearly must approach that of the general population. Its actual relation to the variability of the general population will be shown in the next section.

4. The data obtained from this experiment give no evidence whatever that there is any appreciable correlation between

mother and daughter in respect to egg producing ability. On the average pullets which did exceptionally well as compared with the other pullets in the experiment were just as likely as not to be the daughters of mothers who were exceptionally poor in production as compared with other mothers in the same experiment. In other words, the data so far obtained do not indicate that egg producing ability is sensibly and directly inherited between mother and daughter. There may be such in inheritance, but further data are needed to demonstrate it. The results of the present experiment tend to confirm the conclusion tentatively reached from a study of the past egg records of the Station accumulated during nine years of selective breeding.*

COMPARISON OF "REGISTERED" AND "UNREGISTERED" PULLETS IN RESPECT TO EGG PRODUCTION.

It was pointed out in an earlier section of this bulletin, that in addition to the evidence afforded by a study of the correlation between parent and offspring light on the problem of the inheritance of egg producing ability might be gained by a comparison of the egg production of birds whose mothers were closely selected for high egg production with birds whose mothers were not so particularly selected. Evidence from this source cannot take the place of that afforded by the study of correlation but it may and does supplement such evidence. Besides the so-called "registered" pullets in the present experiment there were 600 pullets which received precisely the same treatment, but whose mothers were birds laying between 150 and 200 eggs in their pullet year rather than birds falling into the "200-egg" or "registered" class. (Cf. p. 51 *supra*.) Of these 600 "unregistered" birds 100 were kept in two pens of 50 birds each, exactly like the pens in which the "registered" pullets were kept. Of the other 500 birds only two flocks—one of 100 and one of 150 birds—are available for strictly fair comparison with the "registered" pullets.

---

* Cf. Pearl, R. and Surface, F. M. A Biometrical Study of Egg Production in the Domestic Fowl. Part I—Variation in Annual Egg Production. (In press). A brief summary of the chief results of this study has been published in Me. Agr. Expt. Stat. Bulletin No. 157.

TABLE VII.

Frequency Distributions Showing the Egg Production of "Unregistered" Pullets. November 1-June 1, 1907-1908.

Eggs Laid.	Number of Pullets Producing each Specified Number of Eggs.					
	House No. 2, Pens 6&7. (50 bird pens.)		House No. 3, Pen 2. (100 bird pen.)		House No. 3, Pen 3. (150 bird pen.)	
	Nov. 1—Mar. 1.	Mar. 1—June 1.	Nov. 1—Mar. 1.	Mar. 1—June 1.	Nov. 1—Mar. 1.	Mar. 1—June 1.
0–2.9	29	–	16	2	30	5
3–5.9	6	2	6	0	17	2
6–8.9	3	1	12	2	17	2
9–11.9	3	2	2	3	6	0
12–14.9	7	1	5	3	7	1
15–17.9	3	1	8	2	5	2
18–20.9	10	2	7	1	10	1
21–23.9	4	0	5	3	10	4
24–26.9	1	1	3	3	11	1
27–29.9	4	0	6	1	3	5
30–32.9	5	1	6	4	5	3
33–35.9	6	2	4	1	4	6
36–38.9	4	3	5	6	7	2
39–41.9	2	2	4	4	4	6
42–44.9	2	2	0	1	4	7
45–47.9	4	6	1	7	2	7
48–50.9	0	4	1	6	2	14
51–53.9	1	9	0	5	1	14
54–56.9	0	5	0	5	0	14
57–59.9	3	5	3	12	2	11
60–62.9	1	12	0	3	0	8
63–65.9	0	4	0	5	1	10
66–68.9	1	6	2	5	0	8
69–71.9	–	10	0	4	1	6
72–74.9	–	4	0	3	–	1
75–77.9	–	1	0	0	–	2
78–80.9	–	2	2	0	–	1
81–83.9	–	1	–	1	–	–
Totals.....	99	89	98	92	149	143

TABLE VIII.

Comparison of the Egg Production of "Registered" and "Unregistered" Pullets. November 1-June 1, 1907-1908.

Groups of Birds Compared.	Mean or Average Egg Production		Variation in Egg Production. Standard Deviation in Egg Production.		Variation in Egg Production. Coefficient of Variation in Egg Production.	
	Nov. 1—Mar. 1.	Mar. 1—June 1.	Nov. 1—Mar. 1.	Mar. 1—June 1.	Nov. 1—Mar. 1.	Mar. 1—June 1.
"Unregistered"—(50 bird pens)	19.38±1.18	53.38±1.30	17.45±.84	18.16±.92	90.02±6.99	34 02±1.91
"Registered"	15.92*±.78	46.83*±.90	16.10±.55	18.10±.64	101.14±6.44	38 66±1.54
Difference	+3.46	+6.55	+1.35	+.06	—11.12	—4.64
"Unregistered" (100 bird pens)	21.43±1.23	45.65±1.36	18.08±.87	19.32±.96	84.37±6.33	42.33±2.45
"Registered"	15.92*±.78	46.83*±.90	16.10±.55	18.10±.64	101.14±6.44	38 66±1.54
Difference	+5.51	—1 18	+1.98	+1.22	—16.77	+3 67
"Unregistered" (150 bird pens)	17.89 ± .87	47.97 ±1.01	15.78±.62	17 84±.71	88 19±5 51	37.19±1 67
"Registered"	15.92*±.78	46.83*± .90	16.10±.55	18.10±.64	101.14±6 44	38 66±1 54
Difference	+1.97	+1.14	—.32	—.26	—12.95	—1 47

* Obtained from the grouped data of Table III and Table IV. The grouping is the cause of the insignificant difference between these averages and those of Table I.

The egg records of such of these 350 "unregistered" pullets as survived the period included in the experiment are shown in Table VII in the form of frequency distributions. The manner in which this table is to be read will be plain from an illustration. From the first column of the table it appears that of the birds kept in 50 bird pens there were 6 whose egg production between November 1 and March 1 fell between 3 and 5 eggs inclusive. Again there were 3 birds in the 100 bird pen whose egg production between March 1 and June 1 fell between 24 and 26 eggs inclusive.

The means and constants of variation deduced from these frequency distributions are given in Table VIII. The data for comparison of "registered" and "unregistered" pullets in respect to their average egg production and in respect to variation in egg production are also given in this table. The differences between "registered" and "unregistered" pullets in respect to egg production are designated as plus when the constant for the "unregistered" birds is the larger and minus when the constant for the "registered" birds is the larger.

From this table the following points are to be noted:—

1. The mean egg production of the "registered" pullets (daughters of "200-egg" hens) is, with a single exception, smaller than the egg production of the "unregistered" birds (not daughters of "200-egg" hens), regardless of the season of the year or of the size of the pens in which the "unregistered" birds were kept. The single exception to this rule is found in the comparison with reference to spring production between the "unregistered" birds kept in a flock of 100 and the "registered" birds. The difference, however, in this case is small and only arises because of the fact that the "unregistered" birds in the 100 bird pen made an exceptionally bad record during the spring months as compared with the other "unregistered" birds. The differences between "registered" and "unregistered" became smaller as the size of the flock in which the "unregistered" birds were kept was increased. During the periods under discussion the birds did not do so well in the large flocks as in the smaller ones.

The lower egg production of the "registered" as compared with the "unregistered" birds (data from 50 bird flocks) is shown graphically in Figs. 12 and 13. These figures give plot-

tings of the data in the first two columns of Table VII and the corresponding frequency distributions for the "registered" birds.

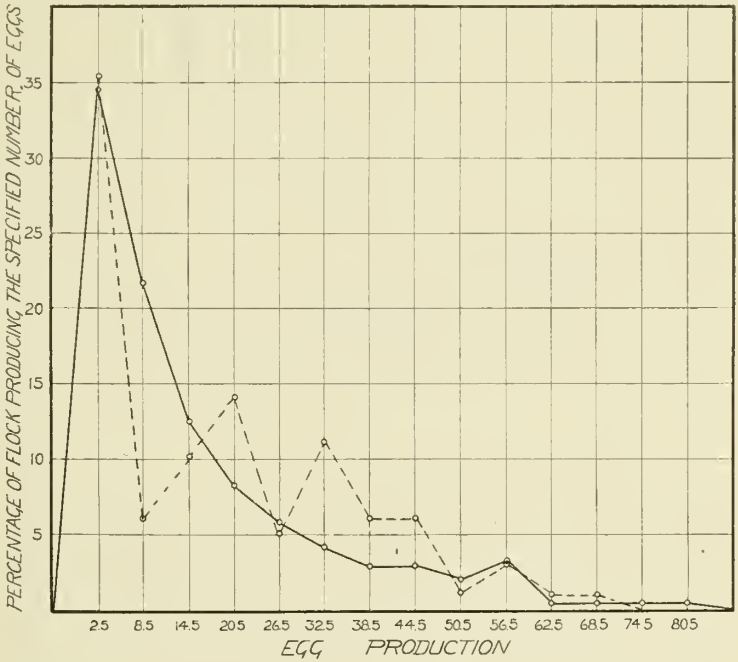

Fig. 12. Diagram showing the egg production during the winter months (Nov. 1 to March 1) of "registered" as compared with "unregistered" pullets. The solid line denotes the "registered" and the broken line the "unregistered" birds. "Unregistered" birds in 50 bird pens.

The same thing is apparent from these diagrams as is brought out by the figures in Table VIII. The lines showing the egg production of the "registered" birds fall generally to the left of the lines for the "unregistered" birds, thus denoting the smaller average production of the "registered."

2. In respect to relative variability as measured by the coefficient of variation, the differences between "registered" and "unregistered" birds are, with one exception, negative. This means that (with the single exception noted) the "registered" birds were somewhat more variable in egg production than were the "unregistered." In other words, contrary to expectation, the group whose ancestry had been most closely selected was actu-

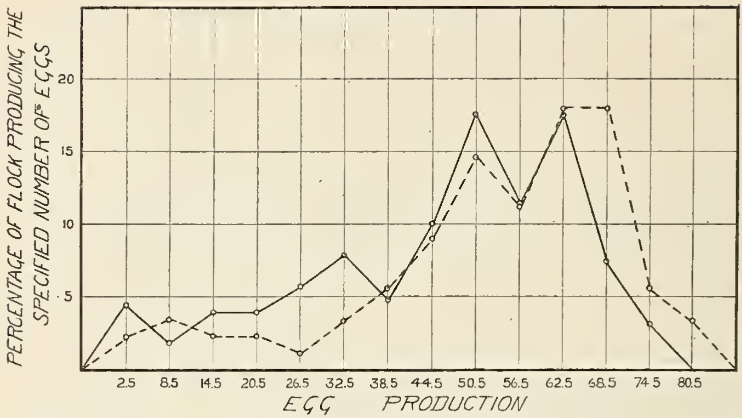

Fig. 13. Diagram comparing the spring (March 1-June 1) egg production of "registered" and "unregistered" pullets. Lines as in Fig. 12.

ally somewhat more variable (i. e., less true to type) relatively than the group whose ancestry had not been so closely selected. The exception to this rule occurs at the point where the exception in the rule regarding the means occurred, namely, in respect to the March to June egg production. The "registered" birds were less variable than the "unregistered" birds kept in the 100 bird flock. This exception, however, only emphasizes the general rule which is to be observed in the other cases. In regard to absolute variability, as measured by the standard deviation, the "registered" birds show a very slightly smaller "scatter" than do the "unregistered" birds. This is to be expected because of the smaller average production of the "registered" birds. The coefficient of variation is clearly the significant measure of variability in the study of egg production, when groups of different average productivity are to be compared."*

3. It will be noted from the values of the probable errors given in the table that some of the individual differences, particularly those between the coefficients of variation can not, when taken singly, be considered significant in comparison with the probable errors. From the practical standpoint this is more than offset by the fact that the differences, whether of means or of relative variabilities are, with the two exceptions noted, all in the same direction.

* Cf. Pearl, R. and Surface, F. M. *loc. cit.*

4. The general result of the comparison of the daughters of "200-egg" hens with other pullets not daughters of "200-egg" hens but receiving the same treatment, feed and care throughout is that the daughters of the "200-egg" hens do not show so high an average egg production as the others. Furthermore, the daughters of "200-egg" hens do not conform so closely to type as do the birds which are not daughters of "200-egg" hens. The significance of these results lies not in the absolute values of the positive differences in the case of the means and of the negative differences in the case of the coefficients of variability, but rather in the fact that they show with the greatest clearness, that daughters of "200-egg" hens on the one hand were certainly not better egg producers than other pullets, and on the other hand certainly did not conform closer to a type in egg production than did other pullets.

DISCUSSION OF RESULTS.

It is proposed to defer to another time and place the detailed discussion of the significance of the results of this investigation in their bearing on the general problem of selection. It need only be pointed out here that, so far as they go, the results of the present work are in entire accord with what has been found in all the extensive and thorough studies made in recent years on the subject of the effect of selection in different organisms. There is rapidly accumulating a mass of evidence that the chief if not the entire function of selection in breeding is to *isolate* pure strains from a mixed population. It is found in actual experience impossible to bring about by selection improvement beyond a point already existing in the pure (isolated) strain at the beginning. This is the result of the long continued extensive and brilliant work of Nilsson * in plant breeding in general. It is the essential result of Johannsen's ** selection experi-

* Cf. DeVries, H. Plant Breeding. Chicago (Open Court Publ. Co.) 1907. Pp. xiii+360.

** Johannsen, W. Ueber Erblichkeit in Populationen und in reinen Linien. Jena (Fischer) 1903. Pp. 68.

† Jennings, H. S. Heredity, Variation and Evolution in Protozoa, II. Heredity and Variation of Size and Form in Paramecium with studies of Growth, Environmental Action and Selection. Proc. Amer. Phil. Soc. Vol. xlvii, pp. 393-546. 1908.

ments with beans. Jennings † reaches the same result in one of the most extensive and thorough studies of the effects of selection ever made. In summarizing his conclusions at the end of the paper (*loc. cit.* p. 522) he makes the following statement: "Certainly, therefore, until some one can show that selection is effective within pure lines, it is only a statement of fact to say that all the experimental evidence we have is against this." Finally, to cite a single further instance, the case recently published by Arenander * showing that true mutants may occur among dairy cattle in respect to fat content of the milk makes it inferentially probable that selection in regard to this character can only bring about improvement by isolation of superior pure strains not by really increasing fat content within a strain.

All together much evidence is accumulating from widely different sources to show that simple selection of superior individuals as breeders will not insure definite or continued improvement in a strain. Some improvement may possibly follow this method of breeding at the very start but the limits both in time and amount are very quickly reached. In support of this view of the possibilities of selective breeding the results of the present paper and of the nine-year selection experiment carried on at the Station furnish definite and positive confirmatory evidence. The experience of the Station shows that in order to establish a strain of hens in which high egg production shall be a fixed characteristic it is necessary to do something more than simply breed from high producers.

In relation to the general subject of the inheritance of fecundity the results of the present work are of considerable interest. This arises in particular from the fact that in statistics of egg production in poultry we are dealing with data measuring the most fundamental factor in fecundity and fertility, namely, ovulation. Practically all of the work which has hitherto been done regarding variation and inheritance of fecundity and fertility has been upon mammals. In all viviparous, as compared with oviparous, animals, the study of these subjects is greatly complicated by the fact that the magnitude of the apparent or recorded productiveness is influenced by

---

* Arenander, E. O. Eine Mutation bei der Fjellrasse (Kullarasse) Jahrb. f. wiss. u. prakt. Tierzucht. Bd. 3, pp. LXXXVII—LL. 1908.

† For foot note to Jennings see preceding page.

several separate and independently varying sets of factors. The unit of such statistics is the individual offspring at birth. But the production of an individual offspring by a viviparous animal implies (1) the removal of an ovum from the ovary (*ovulation*), (2) the *fertilization* of this ovum, and (3) its successful *development* in utero. A considerable proportion of partial or complete sterility in mammals is the result of a failure of the ovum to be fertilized, this failure in no wise depending in many cases on any fault of the ovum itself. The true innate fecundity of the female organism is clearly measured by capacity for ovulation. This is primary, and the other factors concerned in the production of an individual organism are secondary, in so far as the measurement of fecundity is concerned.

In view of these considerations it seems desirable to make use of a more precise terminology than that commonly employed in discussing these matters. We would suggest that the term "fecundity" be used only to designate the innate potential reproductive capacity of the individual organism, as denoted by its ability to form and separate from the body mature germ cells. Fecundity in the female will depend upon the production of ova and in the male upon the production of spermatozoa. In mammals it will obviously be very difficult, if not impossible, to get reliable quantitative data regarding pure fecundity. On the other hand we would suggest that the term "fertility" be used to designate the total actual reproductive capacity of *pairs* of organisms, male and female, as expressed by their ability when mated together to produce (i. e. bring to birth) individual offspring. Fertility, according to this view, depends upon and includes fecundity, but also a great number of other factors in addition. Clearly it is fertility rather than fecundity which is measured in statistics of birth of mammals. The terms fecundity and fertility will be used as here defined by the present authors in future discussions of their work.

As has been pointed out the results of the present investigation do not indicate that there is a sensible inheritance of fecundity from mother to daughter in the mass. Of course, it is not proposed to let the matter rest here; this result will be tested in every possible way. In particular it is important to determine the correlation between mother and daughter in

respect to egg production for a less closely selected group of mothers. Also the question as to whether there does not exist in regard to egg production something corresponding to inheritance in "pure lines" as found by Johannsen in plants. It is possible that this might be the case, without any sensible correlation between mother and daughter appearing in the mass. Further the influence of the male in transmitting fecundity to his daughters needs to be carefully studied. All these problems, and others which they suggest are now under investigation in this laboratory. Individual pedigrees are being kept for all laying birds. Not only is the *performance* in respect to egg production of each individual female tested by trap nests, but the relative ability of each individual both male and female, to *transmit* to their progeny a given degree of fecundity is being thoroughly tested and measured.

In comparing the results of the present study with previous investigations in this field it must be kept in mind that we are here dealing with fecundity *sensu strictu*. The earlier work regarding the inheritance of reproductive capacity has, in all cases known to the authors, had to do with fertility instead of fecundity, using these terms as defined in this paper. Pearson * has shown that there is a positive correlation between parent and offspring in respect to fertility in man and in thoroughbred race horses. Rommel and Phillips ** have shown that a similar correlation exists between mother and offspring in respect to size of litter in brood sows. Pearson *** studying the records of Weldon's mice breeding experiments was unable to demonstrate a sensible parental correlation in respect to size of litter in mice. The only direct positive experimental evidence which has come to our attention showing that fertility in a mammal can be increased by selective breeding is given by Marshall * for

* Loc. cit.

† Rommel, G. M. and Phillips, E. F. Inheritance in the Female Line of Size of Litter in Poland China Sows. Proc. Amer. Phil. Soc., Vol. XLV, pp. 245-254, 1907. Also in abstract; Biometrika, Vol. V, pp. 203-205. 1907.

‡ On Heredity in Mice from the Records of the late W. F. R. Weldon. Part I. On the Inheritance of the Sex-ratio and of the Size of Litter. Biometrika, Vol. V, pp. 436-449, 1907.

** Marshall, F. H. A. Fertility in Scottish Sheep. Trans. Highland and Agr. Soc. of Scotland. 1908. Pp. (of reprint) 1-13.

sheep. He says (p. 12): "Mr. H. C. Stephens of Chalderton, Salisbury, by breeding from twin-bred rams and ewes for some years past, has noticeably increased the fertility of his flock of Hampshire Down sheep." Further details regarding this experiment are given in the original. In general there can be no doubt that there is need for much more extensive and exact experimental and quantitative evidence than we now have before it will be possible to reach any positive conclusion as to the extent and degree of inheritance of fertility among mammals.

SUMMARY.

This bulletin describes the results of an experiment in which "registered" pullets (daughters of "200-egg" hens) are compared (a) with their mothers, and (b) with "unregistered" pullets (*not* daughters of "200-egg' hens, but otherwise of the same breeding) in respect to egg production, when given the same treatment as to housing, feed and the like. These results may be summarized as follows:—

1. The daughters of "200-egg" hens were in this experiment very much inferior to their mothers in average egg production. This is particularly true of winter egg production.

2. This experiment gives no evidence that there is a sensible correlation between mother and daughter in respect to egg production, or that egg producing ability is sensibly inherited. A relatively high producing mother was as likely as not to have relatively poor producing daughters in this experiment.

3. In this experiment the daughters of "200 egg" hens were not such high egg producers as pullets whose mothers' egg records fell in the 150-200 egg class. The daughters of "200-egg" hens were most inferior (proportionately) to the "unregistered" pullets in respect to winter egg production.

4. The daughters of "200-egg" hens were in this experiment somewhat more variable (that is, conformed less closely to type) in respect to egg production than were the "unregistered" pullets. No special stress is to be laid on this greater variability. The significant thing is that the "registered" pullets were *not less* variable than the "unregistered."

It must be remembered in considering these results respecting the inheritance of egg producing ability that they are not to be

regarded as more general than the data on which they rest. The statements which are made above are intended merely to set forth the results of a concrete experiment. They are not at present intended as generalizations applying to all poultry under all conditions. The problem of the inheritance of fecundity wherever attacked is an extremely intricate and difficult one. Further experiments of the same general type as the one described in this bulletin, but planned on somewhat broader lines, are now in progress at the Station and will be carried on for such length of time as is necessary to establish absolutely and beyond all possibility of doubt the answer to the problem with which we are here concerned; namely, whether there is or is not a definite and appreciable inheritance of egg producing ability in the domestic fowl. Until this basic question is definitely answered schemes and rules for increasing egg production by breeding which involve anything further than attention to health, vigor and constitution in the breeding stock, lack foundation in ascertained facts.